Size-Related Obligate and Facultative Parasitism in the Marine Gastropod *Trichotropis cancellata*

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Abstract. The marine gastropod *Trichotropis cancellata*, previously considered to be exclusively a suspension feeder, is also a kleptoparasite, stealing food from several species of suspension-feeding polychaetes. When feeding independently, *T. cancellata* uses its pseudoproboscis, an elongate, ciliated extension of the lower lip, to transport particles captured on its ctenidium to its mouth. When parasitizing, the snail positions its pseudoproboscis in the mouth of a host polychaete and diverts a large proportion of the particles captured by the polychaete to its own mouth. In subtidal habitats around San Juan Island, Washington, most individuals of *T. cancellata* are found in association with the tube openings of suspension-feeding polychaetes. In laboratory experiments, parasitism significantly enhanced fitness in *T. cancellata*. Juvenile snails that parasitized polychaetes grew faster and survived in greater numbers than those deprived of access to hosts, and parasitic adult snails reproduced more than those without hosts. Parasitism in *T. cancellata* and related capulid gastropods may have originated in early post-metamorphic stages as a response to constraints on the efficiency of suspension feeding at small sizes; however, because parasitism is more effective than suspension feeding for snails of all sizes, it now persists throughout life.

Introduction

Animals often vary in trophic mode over the course of their lives. Changes in feeding mechanism at metamorphosis in marine invertebrates are among the most obvious examples of such variation, and are accompanied by major changes in morphology and often habitat. However, equally major shifts in trophic mode can occur without qualitative morphological change. Some of these are related to increases in body size during ontogeny (Werner and Gilliam, 1984). For example, many fishes switch from feeding on individual particles to suspension feeding after reaching a certain size (Gerking, 1994). On shorter time scales, environmental variation may drive changes in trophic mode. For example, some benthic marine invertebrates deposit feed when the flux of particles in suspension is low, but as it increases they switch to suspension feeding (*e.g.*, Taghon *et al.*, 1980; Turner and Miller, 1991). Variation in the concentration or size of food particles may also drive some behavioral switches in trophic mode in fishes (Crowder, 1985; Gibson and Ezzi, 1985; Ehlinger, 1989). Such ontogenetic and behavioral variation is useful for understanding the functional morphology and evolution of feeding mechanisms in at least two ways. First, shifts in feeding mode focus attention on the costs and benefits associated with particular strategies (Werner and Gilliam, 1984; Taghon and Greene, 1992). Second, trophic polymorphisms provide us with excellent models for exploring evolutionary change in feeding mechanisms (Lauder *et al.*, 1989).

Here we describe a case of within-individual variation in feeding mode of interest from both of these perspectives. The marine gastropod *Trichotropis cancellata* (order Neotaenioglossa, family Capulidae) has previously been considered a suspension feeder, generating a feeding current and collecting suspended particles using its ciliated ctenidium (Yonge, 1962). Our results confirm that it is capable of feeding on suspended particles. However, in subtidal habitats *T. cancellata* is frequently found near the tube openings of several species of suspension-feeding polychaetes (Pernet and Kohn, pers. obs.). Here we show that in addition to independent suspension feeding, *T. cancellata* can also efficiently divert and eat particles cap-

tured by these polychaetes. Kleptoparasitism, the diversion of host food to a parasite that does not otherwise damage the host, is well known in some birds, mammals, and terrestrial arthropods (*e.g.*, Elgar, 1993; Vickery and Brooks, 1994; Carbone *et al.*, 1997), and even in one terrestrial gastropod (Zamora and Gomez, 1996), but it is poorly documented among marine invertebrates, with the exception of annelids in the order Myzostomida (Eeckhaut *et al.*, 1995).

We present the results of observations and experiments intended to assess the relative importance of these two trophic modes to *T. cancellata*. These data show that in the laboratory, (i) parasitism of polychaetes leads to substantial fitness gains for small and large individuals, and (ii) small snails cannot meet their basic metabolic needs solely by independent suspension feeding and thus can be considered obligate parasites. Hence, the use and effectiveness of alternate trophic modes in *T. cancellata* depends both on environmental factors (presence of suitable hosts) and ontogenetic factors (body size). The data suggest that Yonge's (1962) hypotheses on the evolution of suspension-feeding neotaenioglossan limpets—in which *T. cancellata* played a role as a model intermediate form—should be reevaluated. Further, our results suggest a novel hypothesis concerning diversification in feeding modes, an important aspect of animal diversity.

Materials and Methods

Collection of animals

Trichotropis cancellata and host polychaetes (Sabellariidae: *Sabellaria cementarium;* Sabellidae: *Potamilla ocellata* and *Schizobranchia insignis;* Serpulidae: *Serpula columbiana* [*cf. S. vermicularis:* Kupriyanova and Rzhavsky, 1993; Kupriyanova, 1995]) were collected by dredging in the vicinity of San Juan Island, Washington, from depths of 30–60 m. Snails and host polychaetes were also observed and collected by divers in the shallow subtidal zone at Shady Cove and Eagle Cove, San Juan Island. Additional sabellids were collected from the breakwater at the Friday Harbor Laboratories, and additional serpulids from the intertidal zone at Argyle Creek, San Juan Island. All animals were maintained in tanks of flowing seawater until used in observations or experiments.

Feeding behavior

For feeding observations, snails and polychaetes were placed in dishes of seawater and viewed with a dissecting microscope equipped with a video camera and recorder. Particle captures were visualized by introducing suspended *Artemia* cysts (~250 μm diameter) or polystyrene beads (40 μm diameter) into the dishes. To estimate the efficiency of *T. cancellata* in parasitizing host poly-

chaetes, we counted the number of particles (*Artemia* cysts) captured by polychaetes and subsequently removed by snails. A parasitized polychaete (*Potamilla ocellata* or *Serpula columbiana*) was positioned so that its mouth was clearly visible through the microscope. When the associated snail began diverting captured particles, we began videotaping. From the videotapes, we were able to count the total number of particles that were (*A*) captured by the polychaete and entered its mouth and (*B*) removed from the polychaete's mouth by the snail. We used the proportion (*B/A*) as a measure of the snail's efficiency in capturing particles from the host.

Suspension-feeding ability in Trichotropis cancellata

To examine the potential for suspension feeding to supply the metabolic needs of *T. cancellata*, we compared the relationships between ctenidium area and body mass in *T. cancellata* and two other suspension-feeding neotaenioglossans, *Calyptraea fastigiata* and *Crepidula dorsata* (family Calyptraeidae). Like *T. cancellata*, *C. fastigiata* and *C. dorsata* use the ctenidium to capture particles from suspension; these last two snails also capture particles with a mucus ''pre-filter'' that stretches across the upstream opening of the mantle cavity (Werner, 1951, 1953). We used ctenidium area as an indicator of suspension-feeding ability because it is positively correlated with pumping rate, one component of feeding ability, in other suspension-feeding molluscs (Møhlenburg and Riisgård, 1979; Meyhöfer, 1985). *C. fastigiata* and *C. dorsata* were collected by divers from Shady Cove. Ctenidium area was measured by dissecting out the ctenidium and tracing its outline using a camera lucida. The tracing was scanned into a computer and the program NIH Image 1.61 (available at http://rsb.info.nih.gov/nih-image) used to calculate its area. The ctenidium and other body tissues (excluding the shell) were then dried at 60°C for 24 h on preweighed foil squares and weighed on a Mettler ARE-100 balance to the nearest milligram.

We used reduced major axis (Model II) regression to describe the relationships between ctenidium area and body mass for the three species (LaBarbera, 1989). All data were ln-transformed. We compared slopes and elevations of these regressions by the Model I method described by Zar (1996, pp. 353–357).

Importance of parasitism to growth, survival, and reproduction

In a direct assessment of the importance of parasitism to several components of fitness in *T. cancellata*, we raised snails in the laboratory with or without hosts and compared growth, survival, and reproduction between treatments. Snails raised with hosts were able to feed by both suspension feeding and parasitism; those raised

without hosts could only suspension feed. We conducted three such experiments, two with small snails (initial shell height 3.0–10.0 mm, measured to the nearest 0.5 mm with vernier calipers) and one with large snails (initial shell height 17.0–23.0 mm). According to Yonge's (1962) data on size and reproductive condition, the small snails were likely immature.

Serpula columbiana served as the host in these experiments; specimens were collected from Argyle Creek on small stones to which they had attached their tubes. Half of the polychaetes were placed into a 7.5% solution of $MgCl_2$ for 48 h, after which their bodies were completely removed from tubes. All stones were thoroughly scrubbed to remove epifauna other than *S. columbiana*. Each stone, now bearing either a single living host or a single host tube without a living occupant, was placed into its own plastic box ($9 \times 9 \times 9$ cm) with walls of plastic screen (mesh size 1 mm). Boxes were submerged in a single tank of flowing seawater, which ranged in temperature from 9° to 13° C over the course of the experiments.

In the first experiment with small individuals of *T. cancellata* (Oct 1995–Jun 1996), 20 snails (initial shell height 4.0–7.0 mm) were distributed among 10 boxes, 5 of which contained hosts and 5 of which contained tubes only. Hence, each box contained two snails and only one host. In the second experiment (Jul 1996–Mar 1997), 40 snails (initial shell height 5.0–10.0 mm) were distributed among 20 boxes, 10 containing hosts and 10 containing tubes only. Again, each box contained two snails and only one host. This distribution of snails (two per host) is seen frequently in field populations (Pernet and Kohn, pers. obs.).

In the single experiment using large individuals of *T. cancellata* (Aug 1996–Mar 1997), 30 snails (initial shell height 17.0–23.0 mm) were distributed among 30 boxes, 15 containing hosts and 15 containing tubes only. In this experiment each box contained only one snail.

Every 4–8 weeks the snails in each box were measured and checked for mortality, as well as for deposition of benthic egg capsules. Growth was calculated as percent increase in shell height. Boxes were cleaned and their positions in the tank were varied haphazardly at each sampling time.

We compared mean growth in the two treatments in each experiment with Student's *t* tests, and survivorship and reproduction with Fisher's exact tests. In the experiments with small snails we could not consider the two snails in a box to be independent replicates, because they shared an experimental environment; for statistical comparisons each box was treated as an independent replicate. Growth rate in each box was calculated as the mean of the growth rates of the snails in the box, and each box was scored as showing mortality if one or both of its resident snails had died.

Results

Feeding behavior

Isolated individuals of *Trichotropis cancellata* feed on suspended particles as described by Yonge (1962). Cilia on the ctenidium generate a current through the mantle cavity. Particles drawn into the mantle cavity with the feeding current are captured on the ctenidium, moved down its filaments, and carried around to the right side of the head in a ciliated food groove on the floor of the mantle cavity. Captured particles, often entangled in a bolus of mucus, are then transferred to the pseudoproboscis, a long, tongue-like extension of the lower lip that is bent under the head to the right, where its tip meets the food groove. The particles are carried up the ciliated pseudoproboscis to the mouth, where the radula is used to pull them into the mouth. The snails consumed 40-μm beads as well as *Artemia* cysts in this fashion.

Snails kept in tanks with a variety of tube-dwelling polychaetes moved onto the worm tubes and positioned themselves near the tube openings (Fig. 1A). Once near a tube opening, snails did not move again unless disturbed. This sessility contrasted with the behavior of snails without hosts; these moved around the tanks frequently. We noticed snails immobile near the tube openings of four species of polychaetes: *Sabellaria cementarium* (Sabellariidae), *Potamilla ocellata* and *Schizobranchia insignis* (Sabellidae), and *Serpula columbiana* (Serpulidae). We did not offer snails other potential host species.

This distribution of *T. cancellata* was also seen repeatedly in the field. Dredged snails were often found attached near the tube openings of sabellariids and sabellids. At Shady Cove, on the east side of San Juan Island, almost all of the many *T. cancellata* seen by divers over a depth range of 5–25 m were found on the tube openings of *Serpula columbiana* (and occasionally of sabellariids and sabellids). Further, host tube openings were frequently attended by as many as five snails. At Eagle Cove, on the west side of the island, almost all of the snails seen by divers were associated with *Sabellaria cementarium*. Again, several snails were often associated with a single host.

We observed interactions between *T. cancellata* and sabellid and serpulid hosts more closely. While host worms were retracted into their tubes, snails used their ctenidia to suspension feed. When the worm's feeding crown eventually emerged from its tube, the snail usually began to probe it gently with its tentacles. This inevitably failed to elicit a reaction from the host, which began feeding, as evidenced by the steady movement of particles down the radioles of the feeding crown and into the worm's mouth. The snail's pseudoproboscis then unwound and lengthened (Fig. 1B) and was inserted into
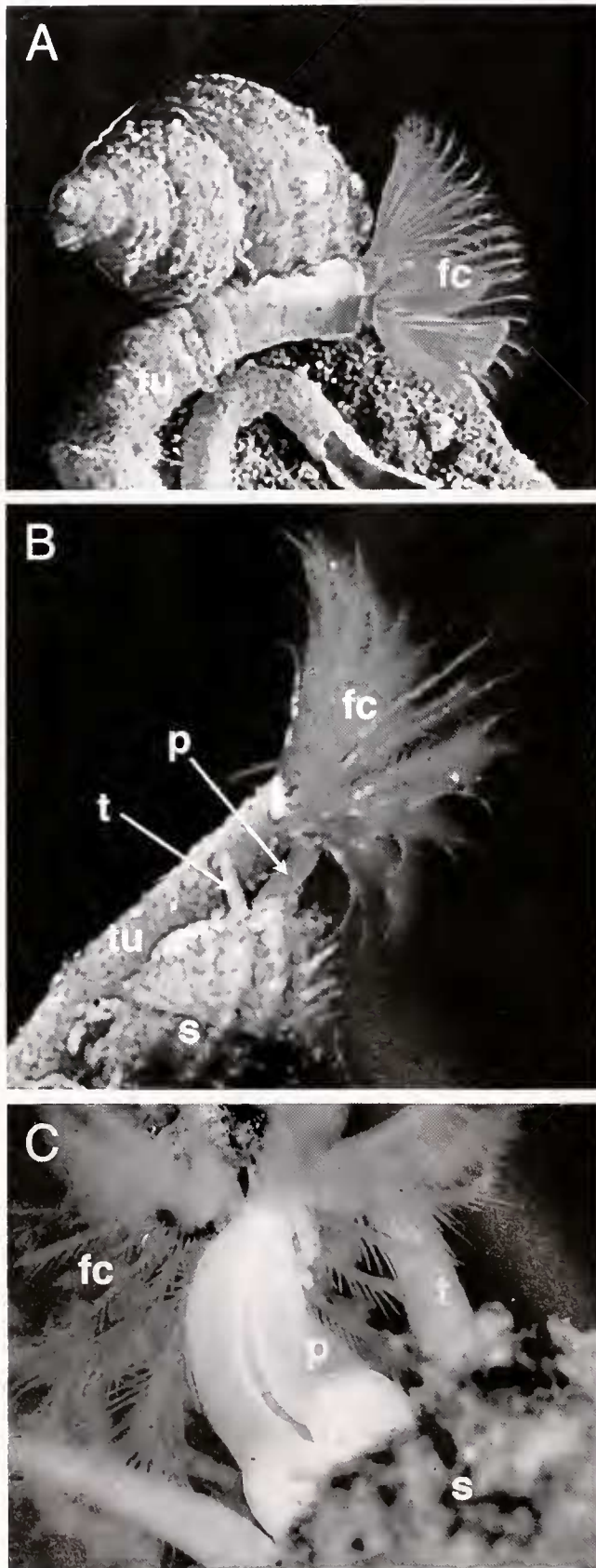
the feeding crown, usually *via* the dorsal or ventral gap between the radioles of the left and right sides (Fig. 1C). The tip of the pseudoproboscis probed around the base of the radioles until it located and slipped into the polychaete's mouth. At this point particles entering the worm's mouth disappeared briefly into its pharynx, but then reappeared traveling in the opposite direction on the snail's pseudoproboscis towards its mouth. This sudden reversal in particle path was seen most clearly (and could be quantified most easily) with large particles (*e.g., Artemia* cysts), but smaller particles and strings of mucus were also pulled from the worm's mouths and ingested by snails.

Snails fed directly from host mouths in this fashion for periods of minutes to hours. Throughout the snails' feeding activities the worms appeared oblivious to their deprivation. Snail feeding was usually terminated by the worm suddenly retracting into its tube, but this withdrawal usually seemed to be related to external events (*e.g.,* disturbance by the investigator) rather than to the behavior of the snail. On several occasions we observed parasitized sabellids briefly rotating their feeding crowns up to 90°; these actions sometimes dislodged snail pseudoproboscides.

Trichotropis cancellata was extremely efficient in removing *Artemia* cysts from the feeding structures of host polychaetes. In the seven short feeding bouts we observed in unique pairs of snails and worms, *T. cancellata* intercepted 100% of the *Artemia* cysts ($n = 10$–40) captured by hosts *Potamilla ocellata* and *Serpula columbiana*.

Suspension-feeding ability in Trichotropis cancellata

Regressions of ctenidium area on body mass for the known suspension feeders *Calyptraea fastigiata* and *Crepidula dorsata* were not significantly different in slope or elevation, so we pooled data from these species for statistical comparison with *T. cancellata*. Over a broad range of body sizes, ctenidium area was significantly smaller relative to body mass in *T. cancellata* than in the

Figure 1. The marine gastropod *Trichotropis cancellata* stealing food from the polychaetes *Serpula columbiana* and *Potamilla ocellata*. (A) *T. cancellata* on the tube of *S. columbiana*, near the crown of feeding tentacles which the worm uses to create a current and capture food particles. *T. cancellata* is also able to suspension feed, using its ciliated ctenidium hidden by the shell in the mantle cavity. (B) *T. cancellata* on the tube of *P. ocellata*. The snail's pseudoproboscis is visible reaching into the worm's feeding crown. (C) A view into the feeding crown of *P. ocellata*, showing the pseudoproboscis of *T. cancellata* entering the mouth of the polychaete, and the snail's tentacles on either side of the pseudoproboscis. Cilia on the pseudoproboscis carry particles from the polychaete's mouth to the snail's mouth. fc = polychaete feeding tentacles, p = pseudoproboscis, s = shell, t = snail tentacles, tu = tube.

two calyptraeids ($P < 0.001$; Fig. 2). Relative growth rates of ctenidia, as indicated by the slopes of regressions of ctenidium area on body mass for *T. cancellata* and the two calpyptraeids, were not significantly different ($0.1 < P < 0.2$).

Importance of parasitism to growth, survival, and reproduction

Experimental snails behaved similarly to other *T. cancellata* observed in the laboratory. In particular, those raised with live hosts moved to the openings of host tubes within a few days of being placed in their boxes, and once on the host tubes, they did not move from them for the duration of the experiment. In experiments with small snails, both individuals in a box settled near the tube opening of their shared host. In contrast, individuals of *T. cancellata* raised without hosts moved around on the walls of their boxes.

In both experiments with small snails, those caged with live hosts grew faster and survived better than those caged with empty host tubes. In the first experiment, snails caged with live hosts showed no mortality over 9 months and increased in mean shell height by 25% (Fig. 3A). In contrast, 5 of 10 snails caged without hosts died, and survivors increased in shell length only 9%. Differences between treatments in both growth (*t* test, $P < 0.05$) and
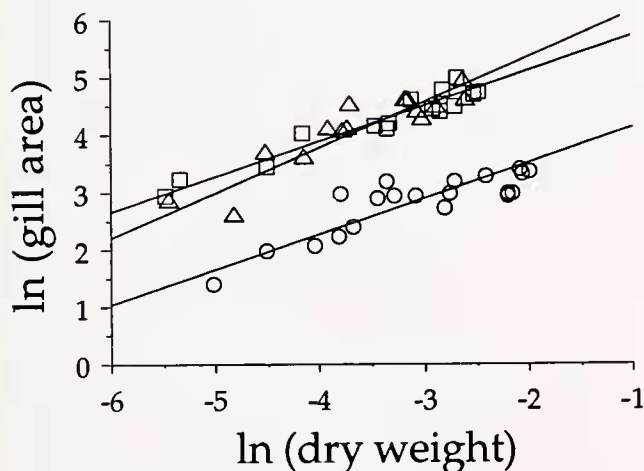
Figure 2. Gill area as a function of dry weight (excluding shell) in *Trichotropis cancellata* (circles, $n = 20$), *Calyptraea fastigiata* (squares, $n = 15$), and *Crepidula dorsata* (triangles, $n = 15$). Lines are reduced major axis regressions of ln-transformed data. Variables (standard error) and coefficients of determination for each of the regressions are *T. cancellata*—intercept 4.649 (0.225), slope 0.593 (0.071), R^2 0.746; *C. fastigiata*—intercept 6.392 (0.333), slope 0.610 (0.089), R^2 0.921; *C. dorsata*—intercept 6.954 (0.171), slope 0.791 (0.048), R^2 0.834. For the regression of pooled *C. fastigiata* and *C. dorsata* data (not shown), the variables and coefficient of determination are intercept 6.607 (0.176), slope 0.692 (0.048), and R^2 0.865.
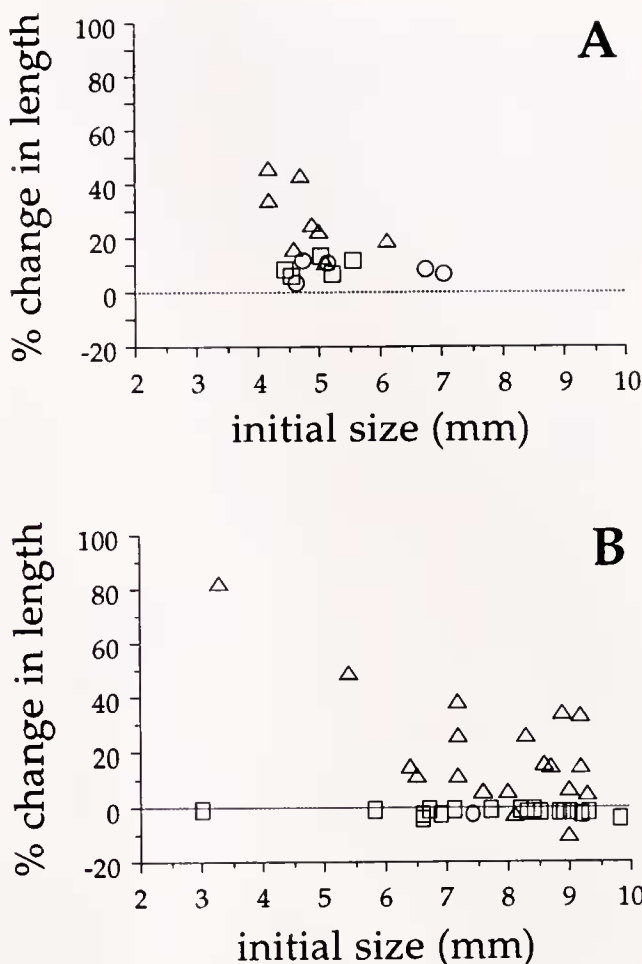
Figure 3. Growth of small *Trichotropis cancellata* maintained in the laboratory with and without living *Serpula columbiana*, measured as percent change in shell height. (A) First experiment. Oct 1995–Jun 1996. *T. cancellata* caged with living hosts (triangles) and with empty host tubes (circles, *T. cancellata* that survived the experiment; squares, *T. cancellata* that died during the experiment). (B) Second experiment, Jul 1996–Mar 1997. *T. cancellata* caged with living hosts (triangles) and with empty host tubes (circle, *T. cancellata* that survived the experiment; squares, *T. cancellata* that died during the experiment).

survivorship (Fisher's exact test, $P < 0.05$) are significant even after sample sizes are adjusted to avoid pseudoreplication. Results of the second experiment were even more dramatic. Here, all snails caged with live hosts survived, and they increased in mean shell length by 19% (Fig. 3B). In contrast, 19 of 20 small snails caged without hosts died, and the single survivor did not grow. The difference in survivorship is highly significant (sample sizes adjusted to avoid pseudoreplication, Fisher's exact test, $P < 0.0001$).

The shell lengths of large snails did not change over the 8-month experiment, whether they were caged with or without hosts. Neither was there a difference in survi-

vorship: 14 of 15 survived the experiment in each treatment. However, the availability of hosts enhanced reproduction of large individuals of *T. cancellata*. Significantly more snails caged with live hosts (7 of 14) deposited egg capsules than those caged with empty host tubes (1 of 14) (Fisher's exact test, $P = 0.03$). All egg capsules contained fertilized, developing embryos, even though none of these snails had had access to mates for at least 6 months prior to capsule deposition.

Discussion

The marine gastropod *Trichotropis cancellata* is able to use two distinct feeding mechanisms, independent suspension feeding and kleptoparasitism of suspension-feeding polychaetes. It employs the former as described by Yonge (1962)—particles are captured on the ctenidium and moved to the mouth *via* the ciliated pseudoproboscis. Parasitism involves inserting the tongue-like pseudoproboscis into the mouth of a suspension-feeding polychaete, where it intercepts particles captured by the worm. Thus *T. cancellata* takes advantage of the large feeding filters of hosts without paying the metabolic costs of generating flow or capturing particles. The frequent association of snails with the tubes of suspension-feeding polychaetes in the field (Pernet and Kohn, pers. obs.) suggests regular use of this feeding strategy.

Several lines of evidence suggest that parasitism is a more important feeding mode than is suspension feeding in *T. cancellata*. First, ctenidial area in *T. cancellata* is significantly smaller relative to body mass than it is in the known suspension feeders *Calyptraea fastigiata* and *Crepidula dorsata*, over a broad range of body sizes (Fig. 2). This result is comparable to that of Meyhöfer (1985), who found that the ctenidial area relative to body mass of a deposit-feeding bivalve was less than those of three suspension-feeding bivalves. The morphology of the ctenidia also differs between the known suspension feeders and *T. cancellata*. The ctenidia of *Calyptraea fastigiata* and *Crepidula dorsata* have the long, filamentous lamellae typical of suspension feeders (Yonge, 1938; Declerck, 1995), whereas the ctenidia of *T. cancellata* have broader, triangular lamellae more similar to those of gastropods that feed by other means (Kohn and Pernet, pers. obs.). These data imply that *T. cancellata* individuals of all sizes are less effective suspension feeders than are members of the Calyptraeidae.

Second, our laboratory experiments show that individuals of *T. cancellata* raised with hosts (and thus able to feed by both parasitism and suspension feeding) are more fit than those raised without hosts (and thus only able to suspension feed). Suspension feeding alone provided insufficient energy to support growth and survival of small snails or reproduction by large snails. These results

should be applied to natural situations with caution, however, because we did not compare the concentration of suspended food particles in the laboratory with natural food levels. If food concentration in our experimental tank was lower than that typically seen in nature (because, for example, suspension-feeding organisms inhabiting the seawater system had depleted incoming water of plankton), growth, survival, and reproduction of snails raised without hosts may have been limited by available food supplies and not by their suspension-feeding abilities. Also, low food levels may have influenced the feeding behavior of serpulids in ways that made parasitism more profitable for snails. For example, low particle concentrations may have stimulated serpulids to feed more frequently, making them available to be parasitized more frequently. Although we suspect that these complications will not alter the main result—that the presence of hosts greatly enhances growth, survival, and reproduction of *T. cancellata*—repeating these experiments in the field is clearly necessary. Preliminary short-term field experiments (E. Iyengar, unpub. data) corroborate our laboratory results that the presence of serpulid hosts greatly enhances growth of small individuals of *T. cancellata*.

Third, the behavior of snails in the laboratory is consistent with the hypothesis that parasitism is more valuable than suspension feeding for *Trichotropis cancellata*. Once a snail finds a host tube, it usually remains there unless it is removed; for example, one *T. cancellata* associated with a *Serpula columbiana* in a laboratory tank did not move from the tube opening for about 11 months (C. E. Mills, pers. comm.). In contrast, snails that are not associated with a host move frequently. Yonge (1962) noted that snails held without hosts invariably move upwards. He interpreted this climbing behavior as an adaptation for enhancing suspension-feeding efficiency by moving to regions of high flow, but it can also be interpreted as a means of locating the tube openings of potential hosts. Although the behavior of *T. cancellata* in the field has not yet been studied, the fact that snails are frequently found on polychaete tubes there is striking (Pernet and Kohn, pers. obs.).

In our laboratory experiments, small snails raised without hosts suffered high mortality, suggesting that they are obligate parasites. In contrast, large snails raised without hosts did not suffer any mortality. What might cause this difference? Declerck (1995) argued that suspension feeding is less efficient in small gastropods than in large ones, for several morphological and mechanical reasons. For example, the ctenidia (and thus the ability to generate flow and capture particles) of small snails may not yet be fully developed. A more fundamental problem with small size may be the increased energy required to generate flow through a mantle cavity of small dimensions. The power required to generate a given volume flux through a

tubular conduit varies inversely with its radius to the fourth power; similarly, the power required to generate a given flow velocity through such a conduit varies inversely with conduit radius squared (Vogel, 1981). For conduits that are not circular in cross-section, these relationships are also inverse (*e.g.,* rectangular conduits: Denny, 1993). Hence, if mantle cavity dimensions increase with body size (*e.g.,* Declerck, 1991), small snails may have to invest relatively more energy than large ones to generate adequate flow through the mantle cavity for suspension feeding.

We observed *T. cancellata* parasitizing four species of polychaetes of three families. This is a minimal estimate of host range, as we did not test other potential hosts. Although our experiments show that parasitism of *Serpula columbiana* is more profitable than independent suspension feeding for *T. cancellata,* the outcome of interactions with other hosts may be different. For example, other host species might have behavioral or morphological traits that might reduce the effectiveness of parasitism. Likewise, though field experiments show that parasitism by *T. cancellata* greatly reduces the growth rates of *S. columbiana* (Pernet and E. Iyengar, unpub. data), the magnitude of such negative effects may vary among host species, for several reasons. Hosts may vary in behavioral parameters like time allocated to feeding, sensitivity to probing pseudoproboscides, and presence or absence of defenses against parasites. Detailed understanding of the effects of *T. cancellata* on its various hosts thus requires more information on the behavioral ecology of suspension-feeding polychaetes (*e.g.,* Wildish and Lobsiger, 1987; Dill and Fraser, 1997), as well as that of *T. cancellata.*

On the basis of his studies of suspension feeding in *T. cancellata* and other gastropods, Yonge (1962) argued that *T. cancellata* might be important in understanding the evolution of suspension-feeding neotaenioglossan limpets. He suggested that limpets such as modern *Calyptraea* and *Crepidula* evolved from an ancestral grazing snail with a typical conispiral shell *via* a suspension-feeding intermediate like *T. cancellata.* Thus suspension feeding preceded the limpet-shaped shell, the latter evolving as an adaptation for resistance to dislodgement in the sedentary suspension feeder (Yonge, 1962). Our data show that *T. cancellata* is not particularly well-suited as a model intermediate in this scenario. *T. cancellata* is not a very effective suspension feeder; parasitism of suspension-feeding polychaetes is likely a more important contributor to its fitness than is suspension feeding. A convincing test of Yonge's hypothesis awaits phylogenetic analysis of the order Neotaenioglossa.

Morphological characters of its larvae and adults suggest that *T. cancellata* is closely related to the members of the genus *Capulus* (Bouchet and Warèn, 1993; Pernet, unpub. data). These are thought to employ both indepen-

dent suspension feeding (Yonge, 1938) and parasitism of other suspension feeders (including bivalves, gastropods, brachiopods, and polychaetes; reviewed by Thorson, 1965). Further studies of the feeding biology of these snails and of their relationships with other neotaenioglossan groups are needed before we can understand the history of these dual feeding modes, but our observations suggest a hypothesis for the evolution of parasitism in capulid gastropods. Ctenidial suspension-feeding molluscs may face constraints on suspension-feeding efficiency when small, for several morphological and mechanical reasons (Declerck, 1995). Some gastropods appear to overcome these constraints by using the alternate feeding mode of benthic grazing at small sizes. As the mantle cavity and ctenidium increase in size with growth, suspension feeding may become energetically more attractive and eventually becomes the primary feeding mode (Declerck, 1995). We suggest that capulid gastropods, including *T. cancellata,* have coped with the high cost of suspension feeding at small sizes by adopting a novel feeding strategy—parasitism of other suspension feeders. The superiority of this parasitic feeding mode for snails of all sizes may explain why it persists throughout life.

Similar size-dependent constraints on feeding efficiency are widespread in animals and may underlie many ontogenetic shifts in trophic mode (Werner and Gilliam, 1984). We suggest that when particular ontogenetic stages adopt novel feeding modes as an evolutionary response to such constraints, the new mode may occasionally supersede the ancestral one throughout the life history, as may have occurred in *Trichotropis cancellata.*

Acknowledgments

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